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LYSICHITON CAMTSCHATCENSE (L) SCHOTT, AND ITS BEHAVIOR IN SPHAGNUM BOGS

Göte Turesson

Lysichiton camtschatcense or the western skunk cabbage can undoubtedly lay claim to greater notoriety than any other herb of the Puget Sound region and the Vancouver strip. Being the only local representative of the aroids and endowed with characteristics strikingly aroidal in nature, it naturally arouses the curiosity of the botanist as well as of the layman. In early spring before other plants show sign of life the pale yellowish color of its peculiar spadix and spathe give life to the dull color of the dormant vegetation. The pleasure, however, is universely proportional to the nearness of the plant. Similar to its eastern congener, the western skunk cabbage enjoys by right the reputation of emitting a stench, comparable in nauseousness to that of a skunk's secretion. Although it is difficult to designate the exact "shading" of the smell, it is an illustrative example of what Kerner (14) in his odor scheme called indoloid. The intensity of the smell is greatest during the period of flowering, and thousands of Staphylinids and carrion flies swarm at this time around the swamps and marshes, attracted by the pungent odor of the skunk cabbage. Later in the season it again attracts the attention by the gigantic size of its leaves, in this region surpassing one meter in length and half a meter in width.

Being typically a plant of swampy places, stream margins and ditches, *Lysichiton camtschatcense* is sometimes found growing in sphagnum bogs under very peculiar circumstances. The clue which *Lysichiton camtschatcense* gives to the interpretation of the physiographic history of one of these bogs will be dealt with below. However, before taking up for discussion the rôle it plays in the past and present history of the bog, it becomes necessary to consider shortly some of its more typical habitats.

The plant societies in which Lysichiton is more or less conspicuous can be grouped in two series: the river series and the pond-swamp series (Cowles, 6). We find Lysichiton present already in the initial stages of the river, *e. g.*, in the ravine. Wherever the topography in the gully admits water to remain during the earlier part of the vegetative season the conditions are favorable for the establishing of Lysichiton. Water-pockets of about three meters' circumference and located in the bottom of a ravine at Maltby, north of Lake Washington, State of Washington, showed the following vegetation (April 1915): *Lysichiton camtschatcense*,[1] *Cardamine pennsylvanica*, *Ranunculus bongardi greenei*. The pools were partly filled with humous material slid down from the slopes together with leaves of the trees in the immediate vicinity, *Acer macrophyllum*, *Alnus oregona* and *Rhamnus purshiana*.

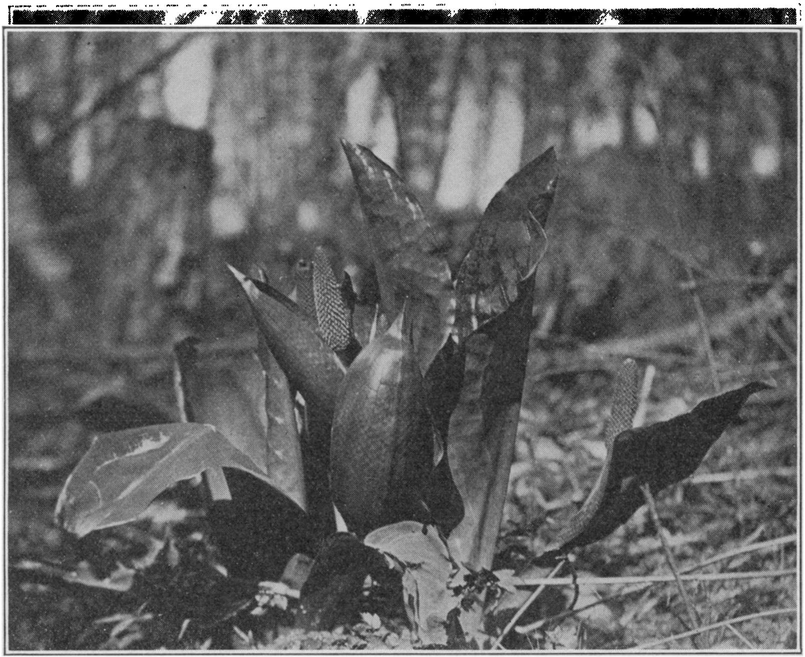

Fig. 1. *Lysichiton camtschatcense* at the time of flowering. Author's photograph.

With the appearance of a permanent stream in the ravine the conditions become still more favorable for Lysichiton. It is true, the erosive action of the stream at first prevents vegetation from gaining a foothold on the streambed, but as the energy of the current is slackened by the accumulation of debris and temporary floodings occur in the wet seasons, a characteristic brookside flora soon appears. *Lysichiton camtschatcense* plays a prominent part in such situations in this region. A representative area from a ravine of the above-mentioned nature was selected at Seattle, Washington, August, 1914, and the plants recorded.

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[1] In questions of nomenclature Piper's Flora of the State of Washington (19) has been followed

Herbs: Agrostis depressa, Athyrium cyclosorum, Cardamine pennsylvanica, Cardamine oligosperma, Cinna latifolia, Circaea pacifica, Claytonia sibirica, Epilobium halleanum, Epilobium adenocaulon, Equisetum telmateia, Geum macrophyllum, Leptaxis menziesii, Lysichiton camtschatcense, Polystichum munitum, Ranunculus bongardi, Ranunculus bongardi greenei, Roripa curvisiliqua, R. nasturtium, Stachys ciliata, Tiarella trifoliata, Washingtonia brevipes.

Shrubs: Echinopanax horridum, Ribes bracteosum, R. divaricatum, Sambucus callicarpa.

Trees: Acer macrophyllum, Alnus oregona.

The steep slopes of the ravine were covered with the following conifers: *Pseudotsuga taxifolia, Thuja plicata, Tsuga heterophylla* and *Taxus brevifolia.*

The later stages in the history of the river, *e. g.*, the establishing of the flood plain make possible a development of Lysichiton unattained in any of the previous stages. As the river grows old and the flow of the water sluggish the deposition of sand and silt becomes more effective. In the extensive mud flats formed in this way along or at the mouth of slow flowing streams, we often find Lysichiton more gigantic in size than anywhere else. The following data have reference to an alluvion of such nature located on the Little Spokane River at Waikiki (May, 1913). The ligneous vegetation was made up of *Alnus tenuifolia, Ribes aureum, R. irriguum, Salix lasiandra caudata, Salix sitchensis, Sambucus glauca, Spiraea menziesii.* The herbaceous vegetation was almost exclusively composed of *Lysichiton camtschatcense.* The mud lay bare between the thickets, and scattered here and there were *Limnorchis stricta* and *Cardamine pennsylvanica.* Typical estival plants were absent, the shade being too dense.

Likewise where wet meadows instead of forest cover the flood plains as is often the case in the Puget Sound region the conditions are very favorable for a luxuriant growth of Lysichiton. The extensive meadows around Bothell mainly composed of *Agrostis depressa,* *Alopecurus geniculatus fulvus*, *Poa pratensis* and *Panicularia pauciflora*, have an abundance of Lysichiton.

In order to make clear the relation of Lysichiton to the pond and swamp vegetation we have to outline briefly the development and succession of the plant societies within the pond-swamp series. The only justification in dealing with this topic so often discussed lies in the fact that no data on the subject have appeared with reference to Pacific coast conditions.

It will be convenient to group the different types of vegetation belonging to the pond and swamp series under two heads, which we for want of better terminology designate as half-drained and undrained ponds and swamps. Both types culminate in the coniferous climax forest, the former indirectly through a deciduous alnetum-salicetum, the latter without the intervention of a deciduous forest stage but through a typical sphagnetum. We find both types well represented in the Puget Sound region. As an example of the first type we may take Union Bay in Lake Washington. The well-known and much-discussed filling up process is going on here with *Nymphaea polysepala*, *Ceratophyllum demersum* and *Elodea canadensis* as the principal soil formers among the aquatic species. Further inland follows the cat-tail Dulichium associations (Transeau 25) with *Dulichium arundinaceum*, *Scirpus occidentalis*, *Sparganium eurycarpum*, and *Typha latifolia*. Back of this association and pushing forward often succeeding in reaching beyond it in places where the water is not too deep we have the two typical marginal plants *Polygonum amphibium* and *Potentilla palustris* fighting for supremacy and overrunning the somewhat earlier established, not seldom pure associations of *Menyanthes trifoliata* and *Hippurus vulgaris*. Next comes the shrub zone with *Salix cordata*, *S. geyeriana*, *S. sitchensis*, *Spiraea douglasii* and *Myrica gale*. There is often standing water between the thickets and pure associations of *Myosotis laxa* and *Oenanthe sarmentosa*. Encroaching upon this shrub zone we have the deciduous forest, almost exclusively made up of *Alnus oregona*. *Salix lasiandra* occurs in spots, and the characteristic shrub stratum is composed of *Cornus occidentalis*, *Lonicera involucrata*, *Rubus spectabilis* and *Sambucus callicarpa*. Scattered trees of *Thuja plicata* give evidence of the advance of the coniferous climax forest on the deciduous forest.

Lysichiton camtschatcense plays a prominent part in some of the successions outlined above, particularly in the alnetum and in the shrub zone. In the former situation it reaches the same gigantic size as in the forested alluvial deposits. Figure 2 shows the spring aspect of an alnetum where some windfalls have occurred (Lake Washington, April, 1914). *Lysichiton camtschatcense* grows here in an *Oenanthe sarmentosa* association with *Agrostis depressa*, *Angelica genuflexa*, *Epilobium adenocaulon* and *Myosotis laxa* as secondary species. A slow-flowing brook empties its water on the northern side and here (not visible in the figure) has a quite different flora established itself. *Roripa nasturtium*, characteristic of such localities, forms an almost closed carpet in which *Lysichiton camtschatcense*, *Agrostis depressa*, *Mimulus moschatus*, *Panicularia nervata* and *Veronica americana* are interspersed.

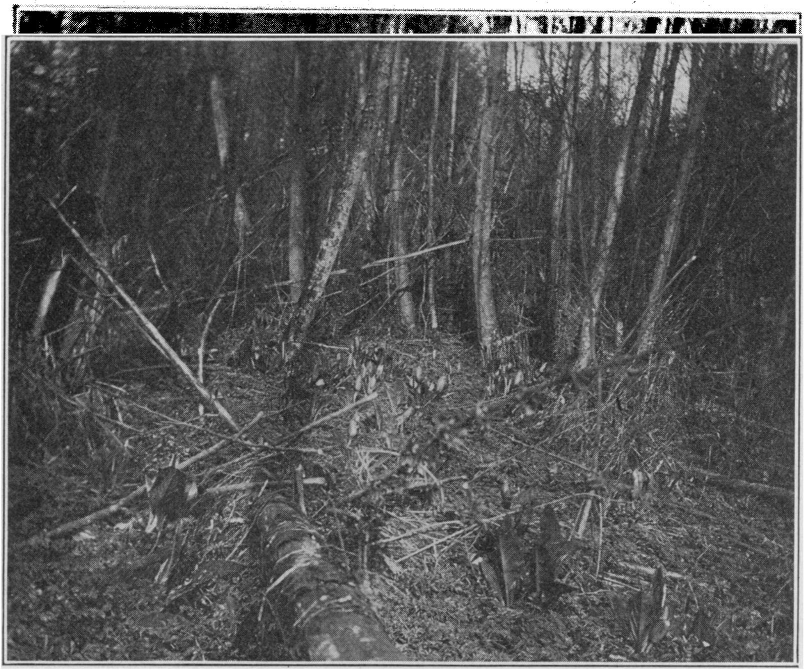

FIG. 2. Alnetum with *Lysichiton* and *Oenanthe sarmentosa*. Author's photograph.

When the topographic conditions are such that complete loss of drainage ensues a series of successions originate which differ radically from those of the half-drained swamp. Bog successions take the place of the former marginal successions and typical peat bogs are built up. In the Puget Sound region where a young topography and a moist climate favor the development of peat bogs, two different types can be distinguished, the second type deviating from the first one in so far as the sedge stage has been eliminated. In other respects the parallelism between the two types is perfect. Both arise and develop from an initial hydrophilous vegetation, both reach the fatal stage inaugurated by the ingress of Sphagnum and, finally, both culminate in the coniferous climax forest.

For an illustration of the first type we may take one of the numerous bogs on Mount Constitution in the San Juan Islands. This particular one is situated in a pocket in the mountain and is about 8 hectares in extent. There is open water in the central parts and a hydrophilous vegetation composed of *Menyanthes trifoliata*, *Nymphaea polysepala*, *Potentilla palustris* and *Chara*. Encroaching upon this vegetation and occupying most of the peripheral parts of the bog we have a typical sedge bog meadow (Dachnowski 8, 9), the low moor, grass moor or sedge moor of Warming (28) mainly composed of Carex. The ground stratum is made up of *Hypericum anagalloides* and mosses, notably *Hypnum giganteum*. The field stratum has the following herbs in addition to the Carex species: *Galium triflorum*, *Mentha canadensis*, *Menyanthes trifoliata*, *Potentilla palustris*, *Scutellaria galericulata*, *Veronica scutellata*, *Viola palustris* and in spots *Lysichiton camtschatcense*. A thick soft mass of Sphagnum occupies a small area in the middle of the bog bounding the open water vegetation. This supports the typical sphagnophilous plants of the region: *Ledum groenlandicum*, *Kalmia glauca*, *Oxycoccus oxycoccus intermedius* and *Drosera rotundifolia*. In places where the sphagnum has been killed, for reasons to be discussed later on, *Philonotis fontana* has stepped in and maintains the same characteristic plants as sphagnum including *Drosera rotundifolia*. That the sphagnum is spreading and will ultimately supplant the sedge vegetation is evident from the fact that small colonies of it have succeeded in establishing themselves among the sedges in advance of the main mass. Seedlings of *Pinus monticola* and *Thuja plicata* are common among the sedges, and dead trunks of *Tsuga heterophylla*, discussed more in detail below, are frequently met with.

The factors that condition the development of the second type

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[1] I am indebted to Professor T. C. Frye for the determination of the mosses.

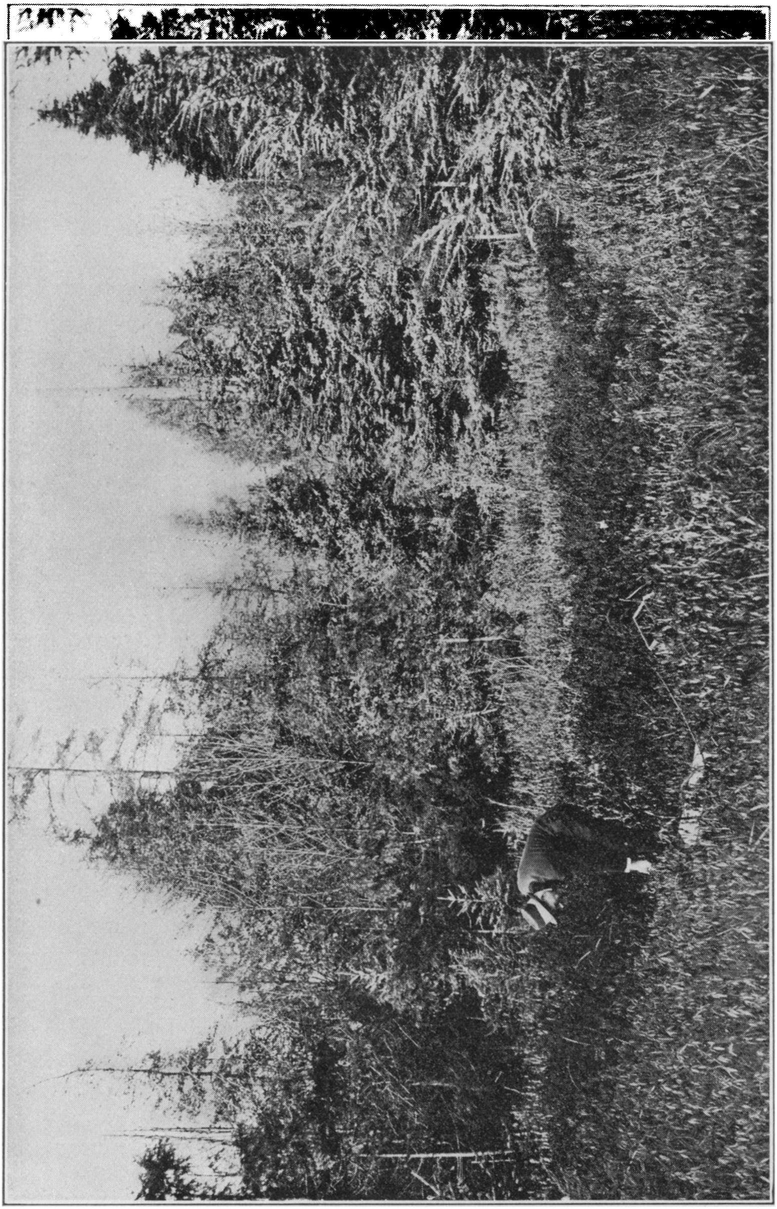

FIG. 3. A corner of Green Cake Bog. Photograph by Y. Westberg.

of peat bogs in which the sedge stage is omitted are the same as those of the first type, and they may all be referred to the lack of drainage. Just why the sedge stage is omitted is not altogether clear. The best example of the type in this region is that of Mud Lake. This lake was once connected with Lake Washington but has in geologically recent times been separated from it by a sand bar thrown up by wind and wave action. Extensive sphagnum bogs occupy the upper end of the lake. These were very likely initiated while Mud Lake still was a bay of Lake Washington. The building up of sphagnum bogs on floating mat vegetation can easily be followed in the southern portion of the lake. *Brasenia schreberi*, *Nymphaea polysepala*, *Potamogeton lonchites*, *P. Nuttallii*, *Utricularia vulgaris* and *U. minor* are very important in shallowing the lake. *Menyanthes trifoliata* is here as in other places (Cooper, 4, MacMillan, 16) the important mat-former by virtue of its mass of intertwined rhizomes. *Potentilla palustris* invades the association, spreads, reaches the edges of the mat and advances out in the open water. Fontinalis, aquatic Hypnum species and other mosses solidify the mat, which next is invaded by *Betula glandulosa* and an undetermined Salix species. Sometimes also *Spiraea douglasii* appears in this stage and often but not always *Typha latifolia*. This is the typical bog shrub stage (Dachnowski, 7, 8). The bog heath stage (Dachnowski, 7, 8) is initiated with the coming in of Sphagnum, which soon smothers the existing vegetation. The former shrubs are crowded out by *Ledum groenlandicum* and *Kalmia glauca* which together with *Oxycoccus oxycoccus intermedius* and *Drosera rotundifolia* establish themselves on the sphagnous substratum. As the xerophytic conditions increase resulting in the drying up of the sphagnum bog in the middle and older parts there is again brought about a change in the composition of the flora. Ledum becomes stunted, disappears entirely from the central parts but persists in the edges bounding the open water. The same is in somewhat less degree true of Kalmia. Cladonia species and *Eriophorum chamissonis* replace them. The bog forest (Dachnowski, 7, 8), is advancing with scattered *Tsuga heterophylla* and seedlings of *Pinus monticola* as forerunners.

The type of bog just described is by far the most common met with in the Puget Sound region. Indeed, the first type, distinguished by the sedge bog stage, is but poorly represented on the mainland. There is indication of such a stage in some places in Mud Lake and also in Spanaway Lake, near Tacoma; but neither is typical of the bog so well represented on Mount Constitution in the San Juan Islands. It might be a matter of difference in age between the bogs on the mainland and those of San Juan Islands, the former having advanced further than the latter and obliterated the sedge bog stage, but there are grounds for the belief that climatic factors are responsible for the dissimilarity.

The San Juan Islands, situated between the Strait of Juan de Fuca and the Strait of Georgia in the northern part of Puget Sound, have a lesser rainfall than most places on the mainland, probably because of the fact that they lie in lee of the Olympic Mountains (Piper, 19). The result is a difference in the flora of the two regions which in some respects is quite remarkable (Piper, 19, Turesson 27).

Many plants characteristic of the drier eastern parts of Washington occur on the islands while they are absent from the intermediate more humid regions. The similarity between the swamp flora of the San Juan Islands and the arid parts of eastern Washington is also great. Indeed, the composition of the swamp vegetation around Sportsman Lake on San Juan Island is almost identical with that of Newman Lake and Liberty Lake of Spokane County in eastern Washington. Both regions are too arid for Sphagnum. It is true, Sphagnum occurs in the northeast corner of Sportsman Lake, but it is not peat forming and cannot exist outside of the protective zone of willow thickets. The southern end of the lake has an extensive association of *Ledum groenlandicum* but Sphagnum is absent. Similarly, the sedge bog meadow on Mount Constitution has great resemblance to the sedge bog meadows in eastern Washington and it is only the slightly higher altitude, and as a result the somewhat greater humidity that makes peat formation through Sphagnum possible on the former locality. However, on the mainland where a more humid climate favors the growth of Sphagnum, the development of the bog becomes altered due to the early ingress of the white moss. The edaphic conditions for a luxuriant growth of Sphagnum are fullfilled already before the establishing of the floating mat vegetation. The interpolation of the floating mat stage of a purely hydrophilous vegetation cannot in itself represent a step towards more xerophytic conditions favoring the growth of Sphagnum and the sphagnophilous flora. These are, as stated above, already in evidence before the floating mat stage has been reached, and the mat merely serves as mechanical support for the Sphagnum and its associates. In Lake Kapowsin, near Tacoma, logs floating in the water have taken the place of the floating mat, and *Drosera rotundifolia*, *Kalmia glauca* and other bog xerophytes flourish in the thin layer of humus covering the logs.[1]

When the rolling sphagnum cover has reached out to the open water bounding the floating mat it plunges down in the water by continual growth from behind thus filling in the pond. This may be seen in many places, for instance, at Mud Lake, Echo Lake and Crystal Lake (compare also Dachnowski, 7, Eriksson, 10). In the latter locality it also succeeds in building extensive mats out into the lake supported by the branches of *Ledum groenlandicum* (compare here Gates, 11).

Some additional facts may be brought out with regard to the various stages in the peat bog vegetation of the region. It is clear that smaller deviations may occur from the development of the two types described in the above. The bog shrub stage, which in this region precedes the bog heath stage, may be wanting or but poorly developed. It is represented by *Spiraea douglasii* in a bog near Maltby. There is also some difference in the composition of the bog forest. The relations of this stage to the climax forest is somewhat difficult to determine as the actual nature and composition of the climax forest is still a matter of conjecture. The demineralization of forest soil due to the humid climate, and the rapid accumulation of humus over the mineral soil layer favor the growth of *Tsuga heterophylla* and *Thuja plicata* while it hinders the development of *Pseudotsuga taxifolia* which thrives best on mineral soils. Undoubtedly, Tsuga and Thuja would together dominate the lowland region of the mainland were it not for the extensive forest fires which by destroying the humus mantle prepare the soil for Pseudotsuga. The belief that the latter tree is excluded from the culminating type of forest vegetation is further strengthened by the fact that Pseudotsuga is unable to seed under its own shade while seedlings and young trees of Tsuga and Thuja are common in the mature Pseudotsuga forest.

With these points in mind the question of the relation of the bog forest to the climax forest, here supposed to be composed of Tsuga and Thuja, will become clearer. The conifers making up the bog forest on the various peat bogs of the region are the following: *Picea sitchensis*, *Pinus contorta*, *Pinus monticola*, *Thuja plicata*, *Pseudotsuga taxifolia* and *Tsuga heterophylla*. Only three of them are important, namely: *Pinus contorta*, *Thuja plicata* and *Pseudotsuga taxifolia*. *Picea sitchensis* and *Pinus monticola* have a very limited distribution in this region. Their occurrence in peat bogs is probably due to lessened competition in the latter localities enabling these species to persist in a region not otherwise favorable to their development. The occurrence of Pseudotsuga in the Green Lake bog, discussed in detail below, is likely to be attributed to the partial drainage of that bog, Rigg (21). Of the remaining, *Pinus contorta* and *Tsuga heterophylla* are especially worthy of notice. Tsuga is always confined to the youngest and wettest peat bogs, in fact, it is the first conifer to appear when the Sphagnum has become firm enough to support trees. When the sphagnum bog gets older and drier Tsuga is killed. The many dried up trunks of Tsuga in older peat bogs or in older and drier parts of a peat bog are remnants from a younger and wetter stage in the history of the bog. The bog forest of the sphagnum bog in its dried stage is a pure growth of *Pinus contorta*. This tree is confined to dry hills and gravelly prairies outside of peat bogs. The occurrence of a plant both on peat soils and on dry, sandy soil has repeatedly been observed in America as well as in Europe and Dachnowski (9) has recently added new examples to the list.

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[1] *Rigg* (22) calls attention to the noteworthy fact that *Drosera rotundifolia*, one of the most typical sphagnophilous plants, occurs outside of the sphagnous substratum in this locality. Its occurrence on a *Philomatis fontana* carpet on Mount Constitution, already referred to, becomes of interest in this connection.

It follows that the relative age of the bog can be determined from the nature of the bog forest. The bogs of Mud Lake with Tsuga and the Crystal Lake bog with *Pinus contorta* are illustrative examples.

The position of *Thuja plicata* with regard to its resistance to dryness seems to be between that of Tsuga and *Pinus contorta*. In eastern Washington and in the Puget Sound region it occurs on dry xerophytic slopes as well as in swamps thus showing the same indifference to habitat as in the Chicago region (Cowles, 6) and approaching in nature *Pinus contorta*. It is not common in the peat bogs of the region (Mount Constitution), but occurs in bogs partially drained.

It is through the two above mentioned stages in the bog forest, the Tsuga association and the Pinus contorta association, that the climax forest will be reached. More extensive investigations have to be undertaken before the course of development after the pine association can be ascertained. As the xerophytic conditions decrease a forest composed of Tsuga and Thuja will in all likelihood establish itself and conclude the series of successions.

Having given a brief account of the nature and character of swamp and bog vegetation in this region we will now discuss in fuller detail the behavior of *Lysichiton camtschatcense* in sphagnum bogs. The bog in which the following observations have been made is that of Green Lake lying within the city limits of Seattle. Most of this bog, formerly about 12 hectares in extent, has been drained and turned into arable soil and only about 0.2 hectare now remain bearing the original bog vegetation. Rigg (21) has in his study of the toxic properties of waters from different sphagnum bogs of the region given a brief sketch of the flora of this bog. From the fact that the water from the bog had no toxic effect on the development of root-hairs in Tradescantia, probably on account of partial drainage, he concludes that plants not found in typical bogs had been able to enter and establish themselves. The flora is doubtless somewhat mixed in character. Figure 3 shows a part of the bog. *Ledum groenlandicum* dominates the area with Kalmia, Oxycóccus, and *Drosera rotundifolia* as secondary species. So far the flora is that of the typical sphagnum bog. However, in addition to the trees commonly found in peat bogs, namely *Tsuga heterophylla* and, in rarer cases, *Thuja plicata*, *Picea sitchensis* and *Pinus monticola*, we find *Pseudotsuga taxifolia* and *Alnus oregona*, and, among shrubs, *Salix scouleri* and *Cornus occidentalis*. The occurrence of these latter might be explained on the basis of partial drainage of the bog. The occurrence of Lysichiton in the bog requires, however, another interpretation. There is, furthermore, another peculiarity which in a still higher degree than the mere presence of Lysichiton demands an explanation. Holes of considerable depth and width are scattered all over the area. Lysichiton is strictly confined to these holes. Firmly rooted in the bottom it occupies most of the space by virtue of its large and numerous leaves which only partly reach out of the hole. In the following table measurements of a number of representative pits are given in centimeters, the width being that of the upper edge.

The form of these holes is mostly circular and wider above than below. Figure 4 is a photograph of one of them in winter-time. Remains of last year's skunk cabbage leaves are seen at the left. The characteristic vegetation of Ledum, Kalmia and Oxycoccus surrounding the pit can also be seen. A further fact to be born in mind is that the hole sunk in the soft mass of Sphagnum has its sides covered not with a growth of Sphagnum but with a number of other mosses and, occasionally, of Cladonia and Peltigera species. The following mosses are found to be common in the upper more exposed parts of the holes: *Dicranum scoparium*, *Hylocomium triquetrum*, *Hypnum cuspidatum* and *Hypnum splendens*. The sides farther down are covered with *Aulacomnium androgynum*, *Brachythecium asperrimum*, *Eurhynchium strigosum* and *Mnium punctatum*.

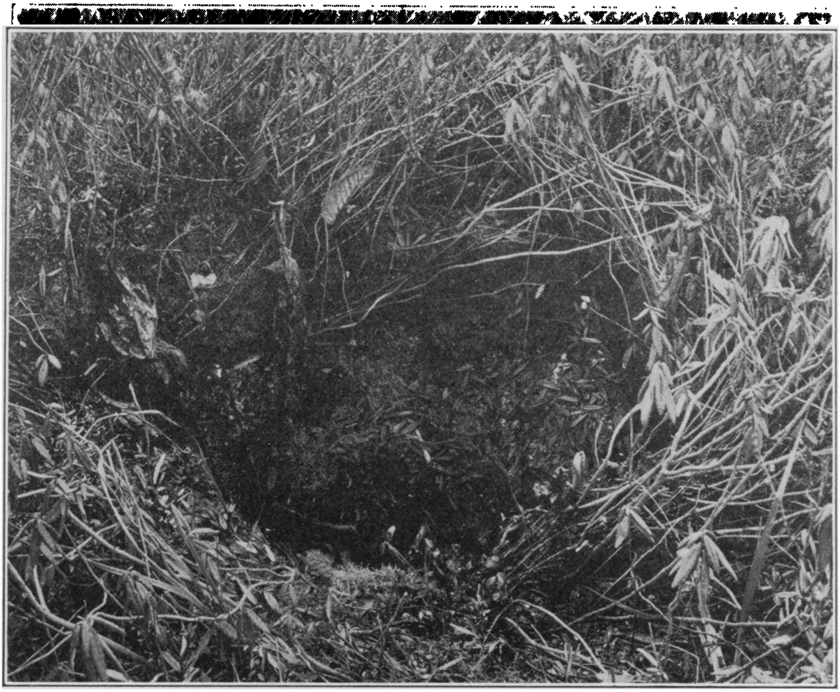

FIG. 4. A skunk cabbage pit, winter time. Photograph by Y. Westberg.

How do these holes originate? Considering the great bulk of leaves produced by Lysichiton in course of the summer and bearing in mind that they rot in winter-time the assumption lies near at hand that the skunk cabbage kills the surrounding Sphagnum. If so, the question as to whether the leaves cause the death of the Sphagnum by the contact itself or indirectly by shading becomes of interest.

In the spring, 1914, a square 1 meter by 1.5 meters in size was laid out in the middle of the bog and decaying leaves of Lysichiton were spread in one-centimeter-thick layer over the selected square.

Another square of the same size was selected and covered with decaying leaves of *Alnus oregona* and *Cornus occidentalis*. When uncovered and examined in the fall the Sphagnum was blackened and apparently killed in both squares. Tufts of this material were brought to the laboratory, put in test tubes partly filled with water and allowed to remain for a month, the water being changed every week. Some of it was put in moist chambers. The moss did not recuperate in either case. Sphagnum planted in test tubes partly filled with water gotten by squeezing decaying Lysichiton leaves grew well. Also when planted in soil collected from the bottom of the skunk cabbage holes Sphagnum showed considerable growth.

The killing of Sphagnum by the skunk cabbage leaves was first thought as being the result of some toxic substance in the skunk cabbage. With the investigation of Baumann and Gully in mind supplemented with those of Skene (24) on the injurious effect of alkalies on the growth of Sphagnum, a number of samples of decaying skunk cabbage leaves were tested. They all gave acid reaction to litmus and phenolphthalein. Any interference with the absorption of mineral salts due to the neutralization of the acid colloids in the hyaline cells of Sphagnum or of the acid medium is therefore out of question. As the leaves of Alnus and Cornus also destroyed the Sphagnum the phenomenon cannot be explained by assuming the presence of a specific toxic substance in the skunk cabbage leaves. The property must be one common to both Lysichiton and Alnus-Cornus leaves.

The cause most likely responsible for the killing of the Sphagnum and which adequately explains both cases is the one of shade and mechanical injury produced by the mass of overlying leaves. That Sphagna are light-demanding plants and very sensitive to waste are well known facts pointed out by almost every worker in the field. Transeau (26) makes the statement that in the Huron River Valley Cassandra affords a very suitable framework for the upbuilding of Sphagnum, among other reasons because its shade does not interfere with the photosynthetic work of the moss. Gates (11) points out that in the bog he investigated the white moss was confined to the margin of the lake "where it is not shaded by grass or bushes." Also Haglund (13) makes the statement that Sphagna are light-demanding plants. As regards their sensitiveness to waste, numerous instances are reported in the literature. Dachnowski (7) notices that covering of fallen foliage suppresses the growth of Sphagnum, Oxycoccus and similar plants. The following is a quotation from Cooper (4): "Because of the shade which Ledum produces and the considerable amount of waste which falls from it, the upward growth of the moss is gradually retarded and finally ceases altogether. About this time or often before, young plants of other mosses more or less tolerant of shade become established upon the higher parts of the Sphagnum moss. *Polytrichum strictum*, *Aulacomnium palustre* and *Calliergon schreberi* soon follow. These species form mats of continually increasing lateral extent which put an effectual stop to further upward growth of Sphagnum." The same facts are brought out in another paper by this author (Cooper, 5). Similarly, Raunkiaer (20) calls attention to the harmful influence of the shady spruce forest on the Sphagnum bog as well as to the injurious effect of leaf fall on Sphagnum. The best illustration of the sensitiveness of Sphagnum to shade is given by Eriksson (10) in his studies on the peat bogs in the middle part of Sweden. It may be cited here. If a spruce has succeeded in establishing itself on top of a Sphagnum hummock in the bog it will ultimately be killed. As Sphagnum is unable to grow in the dense shade below the spruce a depression is formed here. This depression becomes filled with water which results in the death of the tree. Similar "Beschattungs-Schlenken" have prior to Eriksson been described and explained by Sernander (vide Eriksson).

When viewed in the light of these additional data it is easy to see how the deep skunk cabbage pits in the Green Lake bog originated. Sphagnum is unable to grow in the dense shade cast by the large skunk cabbage leaves during the vegetative season. In late fall when the leaves rot, an area all around the plant becomes covered with a thick layer of decaying leaves which smothers and mechanically injures the Sphagnum if it has succeeded in encroaching upon the area dominated by the skunk cabbage. In this way the Sphagnum is kept at a distance, and the pit deepens as the Sphagnum layer continually thickens in the edges not in reach by the skunk cabbage. Finally mosses more tolerant of the deep shade and waste gain entrance and form mats on top of the Sphagnum in the way described by Cooper.

A few additional instances from this region of the sensitiveness of Sphagnum to waste and shade may be cited. It was stated above that Sphagnum had been killed in certain places of the Mount Constitution bog and replaced by *Philonotis fontana.* This was particularly noticeable in the vicinity of Ledum thickets where the shade was dense and waste abundant. An observation somewhat similar to that of Eriksson can be made in the Green Lake bog. Slight depressions are found beneath the hemlocks, the Sphagnum being unable to grow here on account of the shade. The trees are not killed, however, as Tsuga is able to endure very wet soils.

The origin of the marginal ditch surrounding sphagnum bogs in some regions has been discussed from time to time. In order to reach a satisfactory explanation we have to consider not only the factor of shade as expounded by Cooper (4) and Atkinson (1), but also the factor of waste. Fallen leaves and other organic material are swept from the forest floor into the edge of the pool and tend to smother the vegetation (Shaw 23). The combined factor of shade and waste is very likely responsible for the marginal ditch, although suggestions of another nature are made by some. (Burns 3, Gräbner in Warming 28).

It has been shown how Lysichiton is able to hold its own in the sphagnum bog and how as a consequence deep pits are formed. In order to determine more definitely the relation of Sphagnum to Lysichiton and if possible to ascertain in which stage and at what time in the history of the peat bog Lysichiton made its entrance, a cross-section was made through one of the skunk cabbage pits extending one meter beyond the pit and two meters down through the peat. The analyses of the samples of peat brought up from this ditch were supplemented with those made from a ditch already dug in the peat bog for the purpose of draining the bog. To complete the data on the stratification of the bog, test borings were made from the bottom of these ditches. Figure 5 shows the nature of the stratification of this peat deposit.

The area now occupied by the peat deposits is evidently an old lake basin on a bed of drift clay. The outlet of the former lake was obstructed relatively early and the course of development followed that of the undrained swamp. This is confirmed by the entire absence of remains of alder, deciduous shrubs and other plants of the half-drained swamp. That the development has gone through the bog sedge meadow, poorly represented on the mainland at present, is seen from the thick layer of Carex peat overlying the clay. From a wet stage the bog reached a drier stage and big trees grew up. The large stool *in situ* and the remains of *Gaultheria shallon* bear witness of this relatively dry stage. The replacement of the forest by the Sphagnum denotes the critical stage in the history of the bog. The exact cause of the destruction of the forest is very difficult to conjecture. Changes in the level of the ground water is a reasonably safe assumption. Some of the current opinions on this topic will be discussed below. For our interpretation of the past history of Lysichiton in

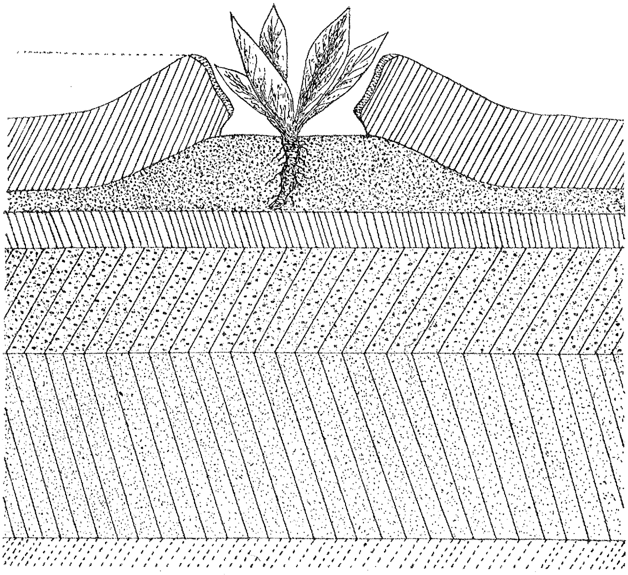

FIG. 5.

A. 60 cm. of ***Sphagnum teres*** peat containing leaves and root systems of the present flora, notably of Ledum, Kalmia and Oxycoccus.

B. 15 cm. of brownish black mud.

C. 20 cm. of ***Sphagnum palustre*** peat containing an abundance of leaves and twigs of Oxycoccus, rarer leaves of ***Tsuga heterophylla***, ***Kalmia glauca***, grasses, and twigs of ***Thuja plicata***.

D. 90 cm. of forest peat consisting of wood detritus and bark mixed with leaves, twigs and cones of ***Thuja plicata***, leaves and twigs of ***Tsuga heterophylla***, leaves of ***Ledum groenlandicum***, ***Kalmia glauca***, ***Gaultheria shallon***, grasses, seedwings of ***Pinus monticola***, and whole plants of ***Camptothecium sylvaticum***. Coal was occasionally met with. One large stool ***in situ*** was found.

E. 150 cm. of Carex peat highly mouldered below with leaves of Kalmia and Ledum, and an abundance of ***Hypnum giganteum***, and sparse Sphagnum.

F. Clay.

G. Moss peat.

the bog the layer *B* is, however, of great interest. This amorphous deposit of a brownish black color has been laid down in water. By some cause or another the bog was flooded and a rich vegetation ensued which gave rise to the mud layer in question. The history of Lysichiton in the bog goes back to the time of the depositing of this layer. When the water subsided, probably while water still remained in the depression during the wet season, Lysichiton established itself. From our acquaintance with its habitat in ravine pools where such mud arises from the decomposition of leaves and other organic material swept into the pool, and through our familiarity with its abundance on alluvial mud banks, we perceive what a congenial habitat such a deposit would afford. It is seen from the cross section that Lysichiton is rooted in this mud layer. The annual decay of great masses of leaves has added to the layer and an extensive mud pad has been built up on top of the original deposit. The second white moss invasion followed and the soft mass of Sphagnum rolled out over the ground occupied by the swamp flora burying and suppressing it with the exception of the skunk cabbage which was able to hold its own against the oncoming white moss by virtue of mere bulkiness. The factors of shade and waste in the formation of the skunk cabbage pits have been discussed above, and the figure makes clear the structure of these pits. During the rainy reason, fall and winter, water collects in the pits, and erosive action loosens the Sphagnum layer from the mud pad resulting in a concavity between the two strata.

Thus the conclusion is arrived at that Lysichiton in the Green Lake bog is a relict from the swamp flora and not related to the group of plants which in recent times have succeeded in entering the bog by reason of partial drainage.

As to the devastation of the forest by Sphagnum indicated in the deposit by the Sphagnum stratum (*C*) overlying the forest bed (*D*), we doubtless evade the difficulties rather than explain them by assuming an alternation of moist and dry periods of great length corresponding to the alternation of strata of Sphagnum and forest in the peat bogs as was done by Geikie (12) and Blytt (2) and after them by Scottish and Scandinavian botanists in particular. The conversion of forest into marsh can take place and be explained without resorting to such bold conjectures. Nilsson's (17) account of the present swamping of the forests in Sweden by Sphagnum is a case in point. Haglund (13) has in a most interesting and convincing way demonstrated that the stools of the forest beds in most of the Swedish peat bogs have been on fire. By burning, the peat became unsuitable for the growth of forest vegetation, while on the other hand Sphagnum found a very favorable habitat and replaced the forest. Furthermore, with the disappearance of the forests an elevation of the level of the ground water takes place and hydrophytic conditions increase, resulting in a corresponding change in vegetation. Burns (3) gives an interesting account of the effect of alternating dry and wet periods of short duration on bog vegetation in the Huron River Valley. His description of the alternating layers of Sphagnum and Polytrichum peat corresponding to the wet and dry periods of previous years is particularly illustrative.

Examples of the destruction of forests under the influence of increased humidity due to local conditions can also be cited from this region. Lake Kapowsin, near Tacoma, originated by the damming up of a river probably by beaver dams and by subsequent swamp vegetation. The surrounding forest was flooded, and the trunks sticking up out of the water bear witness of the flood. Today floating bog vegetation occupies part of the lake's surface. Examples of a somewhat similar nature have been described repeatedly (for instance by Nilsson, 17). The above-mentioned sedge bog meadow on Mount Constitution may also be taken as an example. It occupies a deep pocket in the mountain. In the transition zone between the bog and the adjoining forest almost every tree is killed. The fringe of dead trees is as marked as if cut out with a knife. As the swamp vegetation increased and filled up the concavity it reached the forest which had established itself on the slopes with the result that this was killed either by the water itself or by toxic substances in the stagnant water.

In conclusion I want to call attention to the different ways in which plants enter and have entered the Green Lake bog. In addition to Lysichiton there occurs in the bog an undetermined Carex species which probably also is a relict from the swamp stage. It is usually sterile and illustrates the tendency of plants to become sterile or xerophytic in structure when growing under bog conditions as shown by Lindman (15) and Nilsson (18) for a number of plants and confirmed by the cultural experiments of Transeau (26) and Dachnowski (9).

A point fully as interesting as the relicts in the bog is furnished by the flora that occupies the bottom of the skunk cabbage pits. The nature of the flora which finds shelter here will become clear from the following list of plants found in six different pits.

I. *Angelica genuflexa*, *Limnorchis leucostachys robusta*, *Viola palustris*.
II. *Angelica*, *Galium aparine*, *Trientalis latifolia*.
III. *Angelica*, *Athyrium cyclosorum*, *Gaultheria shallon*, *Spiraea douglasii*.
IV. *Alnus oregona* (seedling) Angelica, Athyrium, *Gaultheria shallon*, *Hieracium scouleri*, *Lonicera involucrata*, *Rhamnus purshiana*, *Sambucus callicarpa* (seedling), *Spiraea douglasii* (seedling).
V. *Athyrium*, *Carex* sp.
VI. *Epilobium adenocaulon*, *Carex* sp. *Potentilla palustris*.

Most of the above mentioned plants do not produce any flowers on account of deep shade and crowded conditions in the pits. However, seedlings of trees often get a start here and some succeed in reaching further development. Many of the trees and shrubs now growing in the bog, as for instance *Alnus oregona* and *Cornus occidentalis*, began in all likelihood their development in one of these pits.

The importance of the skunk cabbage pits and their floras in the replacement of the xerophytic bog flora by a more mesophytic is perhaps greater than it appears to be. There is no doubt, however, that partial drainage of the bog also has played its part in bringing about the present composition of the vegetation.

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